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Digestive physiology and feeding behaviour of equids – a comparative approach

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Introduction

Equids are a family of the Perissodactyla, and thus close relatives to tapirs and rhinoceroses. From a diverse record of fossil equids covering more than 40 genera, a large range of body masses and feeding habits (MacFadden 1992), only seven species of the genus *Equus* survive today that appear (with the exception of coat coloration) as a morphologically relatively homogenous group, covering a much smaller range of body sizes (between 200-500 kg; only the domestic horse breed spectrum appears to approach the body size range covered in fossil times), and sharing basically the grazing feeding niche (Schulz and Kaiser 2012).

Although by no means unsuccessful in terms of standing biomass – considering for example African zebra herds – equids appear much less successful than bovids in terms of species diversity. The difference in the digestive physiology between ruminants and equids is usually invoked for this discrepancy (Janis et al. 1994); the common interpretation is that due to a less severe intake limitation on low-quality forage, equids can subsist in the low-quality forage niche while losing the competition in high- and medium-quality forage niches (Janis 1976; Duncan et al. 1990). Unquantified observations indicate that when forage quality is very low, ruminants lose body condition but sympatric horses are less affected (Abaturov 2005; Koene 2006). Actually, potentially because of different resource use at the sward scale, simultaneously foraging bovids and equids may facilitate optimal resource use for each other (Odadi et al. 2011). An important difference between equid and bovids not related to the digestive system are the longer gestation periods and hence generation times of equids. Because equid gestation periods exceed a year, it is difficult for equids to synchronize births with a seasonal pattern without losing reproductive opportunity, a factor that may make them both more susceptible to predation (Grange and Duncan 2006) and less adapted to highly seasonal environments (Zerbe et al. 2012).

Anatomy of the digestive tract

Tooth morphology

The evolutionary history of Equids is characterised by a molarisation of the premolar teeth and the development of particularly hypsodont (i.e., high-crowned) teeth (MacFadden 1992); hypsodonty is also linked to parallel changes in skull structure, such as a retrograde positioning of the orbita. Hypsodont teeth are associated with the ingestion of abrasive substances, either intrinsic in the

diet as phytoliths, or extrinsic in the form of adhering grit (Damuth and Janis 2011; Kaiser et al. 2013). Inadvertent soil ingestion in grazing horses is demonstrated by the fact that keeping foals off soil (i.e., not allowing them to feed on a pasture) can lead to anaemic conditions (Brommer and van Oldruitenborgh-Oosterbaan 2001), and faecal silica levels corresponding to high hypsodonty were measured in faeces of free-ranging equids (Hummel et al. 2011). The observations that grazing ruminants experience less tooth wear in captivity than in the wild (Kaiser et al. 2009), and that horses on pasture experience less dental pathology than horses kept in stables (O'Neill et al. 2010), match the common observation that horses, evidently equipped for highly abrasive natural diets, experience dental problems associated with insufficient tooth wear when kept as pets (Lane 1994).

Although quantitative comparative data are missing, qualitative comparisons indicate that among both fossil and extant ungulates, equids have particularly complex molar surfaces, also when compared to other perissodactyls (Jernvall et al. 1996).

Gastrointestinal tract

The gastrointestinal tract of all perissodactyls is characterised by a simple stomach and a voluminous hindgut fermentation chamber consisting of the haustrated caecum and proximal colon (Stevens and Hume 1995). The similarity of the digestive tract of the unrelated elephant (e.g. Clauss et al. 2007) represents a drastic example of convergent evolution. A certain degree of bacterial fermentation also occurs in the *Saccus caecus* and the fundic stomach portion of large monogastric herbivores such as horses, rhinoceroses or elephants (Kern et al. 1974; Clemens and Maloiy 1982). In terms of gut capacity, equids follow the general mammal allometry (Müller et al. 2013).

Within the perissodactyls, the equid digestive tract is characterised by two isthmuses or 'narrow points', one separating the caecum head from the proximal colon, and the other separating the proximal colon from the *Colon transversum*; similar structures may exist in tapirs but are absent in rhinoceroses (Clauss et al. 2008a). The relevance of these structures is unclear. In theory, one would expect them to represent delay mechanism to retain digesta efficiently. However, digesta retention in horses is less differentiated, and less long, than in tapirs or rhinoceroses (see below). It was suggested that there is a certain degree of fluid and very small particle retention in the proximal colone of horses (Björnhag et al. 1984); if this was the case, the macroscopic segmentation of the proximal colon might actually help facilitate the comparatively high throughput by reducing losses of bacteria from the fermentation chamber that would otherwise be quickly passed out. For veterinary medicine, these isthmuses represent predilection sites for obstipation colics and may be a reason for the high incidence of colics in domestic and captive wild equids (Ippen and Henne 1991).

Digesta retention, particle size reduction and digestive efficiency

Historically, because of the perceived difference in the intake level between equids and cattle, it has been postulated that ruminants have a low-intake/slow-

throughput/thorough-digestion strategy, whereas hindgut fermenters (such as equids) have a high-intake/fast-throughput/cursory-digestion strategy (Janis 1976). More recently, this view has been modified to better reflect the higher number of studies on ruminants, nonruminant foregut fermenters and hindgut fermenters available today (Clauss et al. 2010a). Hindgut fermenters actually comprise other groups than equids, which can also be categorized as low-intake/slow-throughput/thorough-digestion strategists, such as rhinoceroses and probably tapirs. Equids, therefore, most likely represent a particular strategy within the hindgut fermenters and perissodactyls with particularly short digesta retention times. Equids generally achieve lower digestibilities of forages than ruminants (e.g. Steuer et al. 2013).

Both in hindgut and foregut fermenters, comparative particle size reduction has received little attention until recently. In both groups, a more efficient particle size reduction appears to be associated with a capacity for a higher intake (Clauss et al. 2009b; Schwarm et al. 2009). Because a reduced particle size facilitates higher rates of digestion, increased chewing efficiency allows a reduction in digesta retention, and hence in intake limitation, without compromising digestive efficiency. Among large nonruminant herbivores, equids achieve the highest level of particle size reduction (Fritz et al. 2009), possibly due to their complex molar surfaces (see above). Limited evidence suggests that the digestive tract of horses is tuned to a high food intake, because at very low intake levels, fibre digestion is compromised in spite of correspondingly long digesta retention times (Clauss et al. 2008b).

In passage studies, no or only a very slight difference in the retention of solute and particle markers is evident in horses (e.g. Steuer et al. 2011, with a slightly longer retention time for particles) as compared to other perissodactyls (Clauss et al. 2010b), which appears to contradict the suggestion of selective fluid retention in the proximal colon (Björnhag et al. 1984). Whether this actually means that fluids and particles move more or less simultaneously through the digestive tract, or whether this is a net effect of different processes of particle and fluid retention at different locations in the colon (reviewed in Van Weyenberg et al. 2006), remains to be investigated.

The methane production of horses is lower than that of similar-sized ruminants (Franz et al. 2010) and of a level comparable to that of other nonruminant herbivores (Franz et al. 2011). The reasons for this fundamental difference remain to be investigated.

A peculiarity of equids – and many other hindgut fermenters – is that calcium absorption exceeds requirements, and surplus calcium is excreted via the urinary tract (Schryver et al. 1983; Clauss et al. 2009a). The adaptive value of this strategy remains to be elucidated (Clauss and Hummel 2008).

Food intake and feeding behaviour

Evidence for a difference in food intake level between domestic horses and cattle are scarce; the available data rather suggests similar levels of food intake and similar reduction of food intake in response to increasing forage fibre levels under experimental conditions (Meyer et al. 2010). When comparing data for captive wild equid and ruminant species (Meyer et al. 2010) as well as when

comparing free-ranging horses and cattle in a field experiment (Menard et al. 2002), equids show higher food intake levels than bovids. Similarly, Arnold (1984) and Duncan et al. (1990) observed longer daily grazing times in horses as compared to cows or sheep. In part, this difference may be due to the fact that during ingestion, horses chew more intensively than cattle (Janis et al. 2010); for cattle, rumination is usually not counted as part of the foraging activity. Voluntary food intake of horses on fresh herbage or hays ranges from 50-215 g kg^{-0.75} d⁻¹ (NRC 2007).

Free-ranging equids spend between 50-80 % of the 24-h-activity budget foraging, which by necessity means they forage both during the day and at night (Houpt 2006). Horses usually graze continuously for several hours, which makes a distinct count of 'meal frequency' difficult under natural conditions. This natural feeding behaviour is often linked to stereotypies under less natural conditions, which involve both oral stereotypies (often after a meal of low fibre content) and those linked to the anticipation of the next meal such as weaving or nodding (e.g. Cooper et al. 2005). Free-ranging herbivores use their oral processing apparatus nearly continuously throughout the day, and hardly ever have to adapt behaviourally to absence of food on an hourly basis (Houpt 2006). Therefore, increasing meal frequency in stabled horses may reduce oral, but increase anticipatory stereotypies (Cooper et al. 2005). Another aspect of the natural feeding behaviour of equids is that they move constantly during grazing (e.g. Shingu et al. 2000).

There is a seasonal aspect to feeding activity, which is prolonged in times of low forage availability, and which is suppressed during the hottest times of the day or times of extreme insect harassment, and feeding activity (as well as intake) increase during lactation (Houpt 2006). Free-ranging equids are subjected to seasonal fluctuations in body mass, activity, food intake, energy expenditure and metabolism (Berger et al. 1999; Scheibe and Streich 2003; Arnold et al. 2006; Kuntz et al. 2006; Brinkmann et al. 2012), and behavioural seasonality has also been observed in individually penned performance horses (Bertolucci et al. 2008).

Natural diet

Feral horses and free-ranging wild equids usually consume diets that consist mainly of different grass species, with shrubs, browse or forbs representing minor diet components (NRC 2007). The nutrient composition of the natural diets of horses is therefore easily mimicked by feeding fresh grass (cut or as pasture), or ensiled or dried grass products.

Conclusions

Due to their fossil history of a high but receding diversity, and consistent sympatry with bovids, equids are fascinating objects for studies of evolutionary adaptations. The digestive physiology of horses is tuned to a comparatively high food intake and digesta throughput, facilitated also by a high chewing efficiency. The natural feeding behaviour and diets of equids are relatively well-known, and mimicking natural conditions in captivity is easy in terms of the dietary regime, which would have to consist of forage-only diets. Such diets appear appropriate

for extensively managed captive equids, such as zoo animals, and potentially leisure horses with a low degree of exercise. Deviation from such diets occurs under circumstances of specific demands, such as high-level performance, with potential consequences for physiological and behavioural well-being of the animals that will be covered in more detail in the following contributions.

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